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From field surveys to LiDAR:

Shining a light on how bats respond to forest structure

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ABSTRACT

Detailed information about three-dimensional vegetation structure proves increasingly useful for studying species-habitat relationships in forest ecosystems. This particularly applies to species that make extensive use of the three-dimensional habitat space in forests, such as bats. Bats show considerable variation in flight morphology and echolocation traits that are shaped by habitat features, and are excellent model taxa for investigating relationships between vegetation structure and animal occurrence and movement. The aims of this study were (1) to investigate the relationship between the activity of bats and forest structure and (2) to compare the performance of airborne Light Detection and Ranging (LiDAR) and terrestrial field surveys for measuring habitat features in a representative sample of mixed and deciduous forests in the Swiss lowlands. Leaf-on and leaf-off LiDAR data were used separately, as well as in combination, to evaluate the relative strength of these datasets to describe 3D canopy architecture and vertical forest structure. Field measurements included structural variables such as leaf area index (LAI), vertical layering, snags, as well as shrub and ground vegetation cover. We recorded 145,433 echolocation call sequences from bats and assigned them into three echolocation guilds (short-, mid- and long-range echolocators; SRE, MRE, LRE, respectively) treating separately the dominant species (*Pipistrellus pipistrellus*; Pp). We used Generalized Mixed Effects Models (GLMMs) and applied an information-theoretic approach to assess relationships between guild-specific activity patterns of bats and forest structure in the forest interior, as well as in forest gaps. Standardized coefficients were used to evaluate variable effect sizes and relative importance. We found that guild-specific bat activity was clearly related to three-dimensional forest structure. The activity of SRE, MRE and Pp bats was negatively affected by foliage height diversity, indicating that a large scatter of vegetation elements along 3D forest profiles may restrict accessibility for manoeuvrable bats. Outer canopy surface ruggedness was significantly and positively related to the activity of MRE and LRE bats, as well as Pp, all of which may profit from increased canopy surface ruggedness for foraging (food abundance) and commuting (cover) purposes. The highest variable effect sizes were obtained by combining leaf-on and leaf-off LiDAR data. Leaf-off outperformed leaf-on data, particularly in describing foliage height diversity. LiDAR provided information about bat habitat structure in forests that is not readily available from field surveys.

LiDAR thus increases the scope of inference for future investigations of how species respond to vegetation structure, which can now readily and contiguously be assessed at relevant grain sizes and across large areas.

KEYWORDS

Airborne laser scanning; Bat guild; Chiroptera; Field survey; Habitat structure; Passive acoustic echolocation sampling.

1. INTRODUCTION

In forest ecosystems, vegetation structure is an important biotic factor affecting the presence and abundance of animal species at local scales (Hunter 1999; Tews et al. 2004). Forest vegetation structure and its complexity influence species behaviour and diversity through several mechanisms, e.g. by affecting the availability and diversity of resources and niches, modifying microclimatic conditions, or by providing breeding and roosting sites, shelter or concealment from predators (MacArthur and MacArthur 1961; Melin et al. 2014; Suggitt et al. 2011). The fundamental importance of vegetation and habitat structure for the understanding and maintenance of biodiversity in forests is increasingly recognised (Gustafsson et al. 2012; Noss 1990, 1999), and recent advances in remote sensing may substantially improve our knowledge about relationships between species and habitat structure (Davies and Asner 2014; Simonson et al. 2014).

While forest vegetation structure affects the habitat use of a wide range of taxa (e.g. Zellweger et al. 2015), it is particularly important for insectivorous bats, which use forest habitats for different purposes such as roosting (Ruczynski et al. 2010; Russo et al. 2004), foraging (Patriquin and Barclay 2003) and commuting (Schaub and Schnitzler 2007; Schnitzler et al. 2003). The influence of forest structure on bat activity and occupancy at the stand scale has been well studied in several regions (Adams et al. 2009; Dodd et al. 2012; Erickson and West 2003; Jung et al. 2012; Kalcounis et al. 1999; Müller et al. 2013; Obrist et al. 2011). These studies in general show that regardless of the stratum studied, an increase in vegetation density reduces bat activity (Adams et al. 2009; Brigham et al. 1997; Obrist et al. 2011). However, bats show different responses to vegetation structure depending on their foraging strategy, ecomorphological traits and echolocation call design (Aldridge and Rautenbach 1987; Norberg and Rayner 1987; Schnitzler and Kalko 2001). For example, bat species with low flight manoeuvrability and long echolocation range (e.g. *Nyctalus* spp.) prefer foraging in the open, whereas species with high flight manoeuvrability and short echolocation range (e.g. *Myotis* spp.) make extensive use of the vertical complexity of a forest (Adams et al. 2009; Kalcounis et al. 1999; Müller et al. 2013). These distinct relationships with structural attributes suggest that accurate information of the three-dimensional forest structure is important for better understanding habitat use by bats.

Until the advent of remote sensing technologies, such as Light Detection and Ranging (LiDAR), data collection on stand-scale forest structure was largely restricted to observational field surveys. Apart from being laborious, the availability of field survey data is limited to sample plots, and area-wide evaluations of structural attributes across a range of grain sizes and spatial extents are thus not feasible. Furthermore, field data to study species-habitat structure relationships and to build habitat models are usually collected across relatively small areas. This constrains the scope of inference from such data and poses limitations for many applications in ecology and conservation, which would profit from contiguous and detailed data across a range of scales (e.g. Lindenmayer et al. 2008; Wiens 1989). Moreover, field observations are limited in describing important habitat properties related to the canopy. Fine-scale aspects and variation in canopy architecture and associated vegetation density and surface area, for example, influence the abundance and diversity of spiders and other arthropods (Halaj et al. 2000; Müller et al. 2014). However, such features are difficult to describe in the field and may remain largely concealed from an observer on the ground. Methods that provide objective tools to contiguously depict the entire 3D habitat space in forests and deliver ecologically interpretable variables are thus required to fully appreciate the ecological relevance of forest structure. By providing detailed and contiguous information on habitat structure across large areas, airborne LiDAR has considerably advanced our abilities to meet these requirements. Thus, novel opportunities to study species-habitat structure relationships across a range of scales have emerged and applications of LiDAR are rapidly increasing in number (Davies and Asner 2014; Simonson et al. 2014; Vierling et al. 2008). Based on structural attributes such as vertical complexity, canopy height and heterogeneity, LiDAR has frequently been applied to study bird diversity and habitat use in forests (Bradbury et al. 2005; Clawges et al. 2008; Goetz et al. 2007; Hinsley et al. 2006; Lesak et al. 2011; Zellweger et al. 2013). The diversity and activity of other taxonomic groups, such as arthropods, is related to LiDAR-derived canopy architecture and indicators of microclimatic conditions in the lower stratum of forests (Müller et al. 2014; Müller and Brandl 2009; Vierling et al. 2011). Despite the strong dependence of bats on forests, studies using airborne LiDAR to investigate how bat behaviour is related to forest structure, however, are still relatively rare (Davies and Asner 2014). Jung et al. (2012) found a strong relationship between bat occurrence and

activity and structural heterogeneity related to canopy and edge characteristics in different managed forest types. Fabianek et al. (2015) found that a high proportion of LiDAR-derived canopy gaps within mixed and coniferous forests positively affected roost selection by male *Myotis* bats in Canada, and ground-based LiDAR has provided insights into the flight behaviour of big brown bats (*Eptesicus fuscus*) in a deciduous forest (Yang et al. 2013). Furthermore, the potential of LiDAR to complement field surveys by delivering unique information on structural habitat attributes, as well as potential benefits from using a combination of leaf-on and leaf-off LiDAR data to measure habitat structure remain to be explored. Given the increased canopy penetration of laser pulses during leaf-off conditions, we expect it to carry essential information about subcanopy vegetation elements potentially affecting the manoeuvrability of bats. Outer canopy and edge characteristics, however, may be more accurately represented by leaf-on data, hence a combination of leaf-on and leaf-off data provides ecologically valuable information in deciduous and mixed forests, such as the ones studied here.

The aim of this study was to test the assumption that forest vegetation structure strongly affects bat activity and that this relationship depends on species' eco-morphological traits such as flight manoeuvrability and echolocation call design. Such effects should thus be specific for guilds consisting of short- (SRE), mid- (MRE) and long- (LRE) range echolocators. We used a set of variables representing structural forest attributes from both field and LiDAR surveys, and investigated their effect on guild-specific activity patterns in mixed and deciduous forests. The main objectives were (i) to determine key structural variables that influence bat activity at the guild level and (ii) to compare the performance of terrestrial field and LiDAR surveys of forest structure and (iii) to investigate the relative strength of leaf-on and leaf-off LiDAR, as well as a combination thereof for providing unique information on forest structural attributes affecting bat habitat use.

2. MATERIAL AND METHODS

2.1. Study area

The study area was situated in Central Europe in the northern part of Switzerland, at the interface between the lowlands and the Jura Mountains (Canton of Aargau: 47°14'–47°62'N, 7°71'–8°46'E, 260-910 m a.s.l.). The average annual temperature and rainfall in this region are 9.7°C and 1076 mm, respectively (www.meteosuisse.admin.ch). The landscape consists of a mosaic of fragmented habitats such as forests (37%), agricultural land (45%) and urban areas (15%). The most abundant forest tree species are *Fagus sylvatica* (32%), *Picea abies* (26%), *Abies alba* (14%), *Quercus* spp. (7%) and *Fraxinus excelsior* (7%).

We applied a stratified-random sampling design to select eight 1-km^2 cells that were characterised by more than 50% of temperate forest cover (Figure 1). Each cell contained four randomly selected forest plots. Forest plots included both forest interior habitats and forest gaps, and were located within deciduous (covered with more than 66% deciduous trees) or mixed (covered with between 33 and 66% deciduous trees) forest stands. We defined the forest gap as an open area within a forest where the canopy cover was considerably lower than in the surrounding forest areas (Runkle 1992). We identified forest gaps during field investigations; the minimum size of a forest gap was 400 m^2 (mean 1,318 m^2). The distances between the recording sites in the forest gap and the forest interior ranged from 46 to 140 m (mean 81 m). To avoid biases from potential edge effects, the plots were located at least 50 m away from outer forest edges, and at least 20 m away from forest roads (for details, see Froidevaux et al. 2014).

2.2. Bat echolocation call recording and identification

Sampling took place between 4 June and 29 August 2013 (71 full nights) when weather conditions were optimal, i.e. during dry nights with a minimum temperature ≥ 7 °C, conditions that are suitable for insect flight and consequently for activity in aerial-feeding bats. We digitally recorded bat echolocation calls at 312.5 kHz sampling rate and 16 bits depth with 12 ultrasound detectors (BATLOGGER; Elekon AG, Lucerne, Switzerland), each protected by a Strongbox (Elekon AG, Lucerne, Switzerland). Microphones were water resistant, omnidirectional and sensitive between 10

and 150 kHz (± 5 dB). We programmed detectors to automatically record bats throughout the night (from sunset to sunrise, 21:30 h – 05:30 h).

We allocated three detectors per forest plot, one located in the centre of the forest gap mounted on a pole at a height of 1.35 m, and two in the forest interior. There, we placed one detector on a pole at 1.35 m height, and another detector up in the canopy at a mean height of 18.9 m, using a slingshot, rope and pulley system. We developed this design to better account for the vertical habitat use of bats in forests (Adams et al. 2009; Kalcounis et al. 1999; Müller et al. 2013). In total, each forest plot was sampled between 6 and 12 nights throughout the field season. This extensive sampling effort considerably increased the accuracy and completeness of data on bat activity (Froidevaux et al. 2014).

We identified bat echolocation calls using BATSCOPE, a semi-automatic bat identification software package (Boesch and Obrist 2013). The process consisted of extracting 23 relevant numeric variables from call spectrograms (0.31 kHz x 0.16 ms resolution) and comparing these with variable values from 19,636 reference calls from 27 European species (Obrist et al. 2004). Based on three classifiers (*Support Vector Machine*, *K Nearest Neighbours*, *Quadratic Discriminant Analysis*), calls were then classified into species with an average correct classification rate of 95.7% when all three classifiers agreed (i.e. 76.4% of the cases; predictions obtained from 10-fold cross-validation; see Boesch and Obrist 2013). We then verified bat call sequences (i.e. series of echolocation calls) to taxonomic entity using the semi-automatic processes provided by BATSCOPE, which implements multiple filter combinations to reach the taxonomic level most appropriate for identification (for details, see Froidevaux et al. 2014). According to their affiliation (i.e. species, complex of species, genus, complex of genera), we grouped bats into different guilds reflecting their echolocation range (Aldridge and Rautenbach 1987; Schnitzler and Kalko 2001; Schnitzler et al. 2003), namely short-range echolocators (SRE; *Myotis* spp. and *Plecotus* spp.), mid-range echolocators (MRE; *Pipistrellus* spp. and *Hypsugo savii*) and long-range echolocators (LRE; *Eptesicus* spp., *Nyctalus* spp. and *Vespertilio murinus*) (see Table 1 in Frey-Ehrenbold et al. 2013 for more details). As *Pipistrellus pipistrellus* largely dominated the MRE guild (84.1 % of sequences), we excluded this species from the guild and analysed its activity pattern separately.

194

195 **2.3. Assessment of forest structure**

196 2.3.1. Field survey

197 We conducted field measurements on forest structure in July and August 2013, when trees
198 were in full leaf. To collect data in the forest interior, we defined a stand around each forest ground
199 site where the bat detector was placed, measuring an area of 30 x 30 m, by using poles and a laser
200 distance meter (LEICA, Disto D8) and aligned it parallel to the terrain's slope. Each stand was then
201 divided into four quarters (15 x 15 m) to optimise precision during data collection (e.g. estimation of
202 shrub cover). Similarly, forest gaps were delimited by the tree lines and divided in four equal parts
203 with a compass. Following the methodology of the Swiss National Forest Inventory (Keller 2011), we
204 surveyed seven forest variables for the forest interior and five for the forest gap, each representing the
205 local vegetation structure (Table 1). To minimize any observer bias, the same person (J.S.P.
206 Froidevaux) collected all the data.

207 The degree of understory vegetation density was measured from the centre of the forest stand
208 with a profile board (Nudds 1977), which was placed subsequently in the four corners of the stand.
209 The leaf area index (LAI) was used as a surrogate of the combined cover of both the canopy and the
210 subcanopy strata. We calculated the LAI with the program Hemisfer 1.5 (Schleppi et al. 2007;
211 Thimonier et al. 2010) from five hemispherical photographs that were taken in the centre of each 15 x
212 15 m quadrat of the forest stand. In forest gaps, the structure of the edge was classified as either open
213 or closed (Hamberg et al. 2009), based on visual inspection, and the gap size was calculated using
214 ArcGIS Desktop v10.

215 2.3.2. LiDAR metrics

216 We used discrete multiple return airborne LiDAR data to compute a number of metrics
217 describing forest structural properties that are ecologically relevant to bats (Table 1). Milan
218 Geoservices GmbH acquired raw data for the study area twice in 2014, once during leaf-on and once
219 during leaf-off conditions. The data were acquired using a RIEGL LMS-Q680i airborne laser scanner
220 flown at an average altitude of 700 m a.s.l. and average flight speed of 110 km h^{-1}, with a beam
221 divergence of 0.5 mrad. The overlapping flight strips and a pulse repetition frequency of 300 kHz led

to an average pulse density in each dataset of 7.5 pulses/m^2, resulting in an average echo density of 22 pts/m^2 across all plots. Comparison with 30 reference points from terrestrial measurements revealed an average vertical accuracy of 3.1 cm.

We merged the data from both flight missions and used a suite of LAStools algorithms (Isenburg 2013) involving point classification and triangulation to calculate a terrain model, which was then used to calculate the terrain-corrected (normalized) vegetation heights. We used the normalized point clouds of the leaf-on and leaf-off data sets separately, as well as the combination thereof to investigate the relative strengths of these different LiDAR datasets and whether they provide unique and complimentary structural information compared to field vegetation surveys. For each of the three LiDAR datasets we computed nine variables describing forest vegetation structure with potential relevance to bat activity, applying a height threshold of 1.3 m to identify vegetation points (Næsset 2002) (Table 1). Canopy height was computed as follows: we gridded the vegetation heights using a cell (pixel) size of 0.5 m, retained the highest available point per cell and assigned its height to the respective cell, thus representing the upper canopy surface. None of the point clouds contained returns from infrastructure such as power lines or buildings. Canopy ruggedness was calculated using the terrain ruggedness index (TRI), algorithm (Wilson et al. 2007). Canopy ruggedness measures the local variation in canopy height by comparing a central pixel with its neighbours, taking the absolute values of the differences, and averaging the results (Wilson et al. 2007). Variation in outer canopy height and associated edge characteristics may be important for bats because it affects their foraging and commuting behaviour. We derived this variable for both the forest interior and the gap, and used the same nomenclature (i.e. canopy ruggedness) for the two. However, we are aware of the fact that in forest gaps, this variable represents the ruggedness of the upper vegetation surface, which may not always be referred to as canopy. To describe the degree of scatter of vegetation elements along the vertical forest profile, we adopted the foliage height diversity (FHD) concept proposed by MacArthur and MacArthur (1961). We defined FHD as

$$\text{FHD} = H' = -\sum p_i \ln p_i,$$

where *H'* is the Shannon–Wiener information index and p_i is the proportion of vegetation points in the i^{th} height interval. We calculated four equal height intervals (i.e. horizontal bands) delineated by the quartile heights of the vegetation point cloud (cf. Clawges et al. 2008).

Each variable was calculated for the field plot dimensions, and spatial co-registration was undertaken based on the averaged coordinates from at least three GPS recordings, using a GARMIN GPS device (GPSMAP 62st). The accuracy of the GPS localization varied in average 2.7 m in the gaps and 3.7 m in the forest interior. Given that the distance at which a bat can be detected is species specific, typically in the range of 10 to 50 m, these GPS values were sufficiently accurate to subsequently describe the habitat structure relevant to bats.

2.4. Statistical analyses

Bat guild activity per night was measured by counting the number of 5 min intervals where bat sequences of a given taxon were recorded. This time period limits possible bias arising from the fact that single bats may forage in the recording range of a microphone for extended times. Acoustic data from the forest ground sites were previously pooled with those from the corresponding canopy sites to get a single activity index for the forest interior. We applied the Mantel test for testing the spatial independence of the total bat activity data by using two distance matrices, namely (i) the spatial distance between the sampling sites and (ii) the distance between the bat activity indexes measured at the given sites. No spatial autocorrelation was found (Mantel statistics: $|r| = 0.04$, *empirical p.value* = 0.17, with 999 permutations). To assess the relationship between guild-specific bat activity (dependent variable) and vegetation structure (independent variable), we used generalized linear mixed models (GLMMs) (function *glmer*, R package *lme4*) with the appropriate distribution: Poisson for LRE guild and negative binomial for SRE and MRE guilds, as well as for *P. pipistrellus*, due to overdispersion in the data. Mean night temperature and forest variables were considered as fixed effects whereas the number of location-replicates and nights were implemented as random effects to avoid pseudo-replication. Before integrating the forest variables into the models, we investigated any correlations among variables using Spearman's correlation test. Each variable was standardized to obtain the same unit measures and enable a comparison of variable importance based

276 on the effect sizes in the GLMMs. When correlations were found ($|r|>0.7$, Table S1), we kept only the
277 variable with the highest ecological significance to explain bat activity. Moreover, if correlated
278 variables had equal ecological importance, we tested them independently within our models to select
279 the variable with the most explanatory power. Finally, to identify the most parsimonious model we
280 applied an information-theoretic approach using Akaike's Information Criterion corrected for small
281 sample sizes (*AICc*), and chose the model with the fewest parameters when models were considered
282 equivalent ($\Delta AICc < 2$) (Burnham and Anderson 2002). Statistical analyses were performed using R
283 3.0.1 (R Core Team 2013).

3. RESULTS

A total of 145,433 bat sequences containing 2,064,188 bat echolocation calls were recorded over 71 nights, including 113,340 sequences belonging to *P. pipistrellus*. 112,822 sequences (99.6%) could be affiliated to a guild. We assigned 68% of them to the MRE guild, 30% to the SRE guild, and 2% to the LRE guild. While nocturnal activity (i.e., number of 5 min intervals where sequences of a given taxon were recorded) of SRE was higher in the forest interior than in forest gaps, the opposite was true for MRE and LRE, in spite of the fact that we sampled both at ground and canopy level in the forest interior (Table 2). Only 5-10% of all echolocation call sequences recorded contained terminal buzzes indicative of feeding behaviour (Griffin et al. 1960). Thus, we were unable to separate feeding behaviour and commuting behaviour in our analysis.

The effect of vegetation structure on bat activity was guild-specific, as revealed by the different variables and effect sizes in the GLMMs (Table 3). In the forest interior, the activity of SRE increased with decreasing FHD and density of trees. However, with the leaf-off and combined LiDAR datasets we found a comparably larger negative effect of FHD for MRE and *P. pipistrellus*, both of which responded positively to increasing canopy ruggedness and negatively to the LAI. LRE activity increased with increasing mean canopy height and was positively associated with increasing temperature.

In gaps, the activity of SRE increased with increasing ground vegetation cover, whereas MRE and LRE activity increased with increasing mean vegetation height and canopy ruggedness, respectively. *P. pipistrellus* showed the same trend as the MRE guild.

Significant effects of forest structure on bat activity were revealed by four LiDAR variables (i.e. FHD, canopy ruggedness, mean canopy height, and mean vegetation height), which were more often retained than the three significant variables measured in the field (i.e. density of trees, LAI and ground vegetation cover) were retained. The combined leaf-on and leaf-off dataset performed best in describing structural variables related to bat activity. This was particularly evident for FHD and canopy ruggedness, where the variable effect sizes were generally larger compared to the results of either leaf-on or leaf-off data. Leaf-off data represented the effect of FHD on SRE, MRE and *P. pipistrellus* activity better than leaf-on data. Although canopy ruggedness from leaf-on data was not

312 retained for MRE and *P. pipistrellus* (Table 3), canopy ruggedness frequently occurred in the top

313 models in the leaf-on model selection for MRE and *P. pipistrellus* (Table S2).

4. DISCUSSION

4.1. Vegetation structure affects bat habitat use

Our results indicate a strong effect of the three-dimensional structure of forests on bat activity at the stand scale, and that this effect depends on guild-specific traits. Bat habitat use, in addition to foraging strategy, is mainly constrained by their echolocation call design and ecomorphological characteristics (Schnitzler and Kalko 2001; Schnitzler et al. 2003). The activity of SRE, for example, was higher in the forest interior, suggesting that bats that emit short-range echolocation calls and manoeuvre well with their low wing loadings, may be better adapted to forage in the forest interior than bats with a high wing loading and corresponding high flight speed, low manoeuvrability and long-range echolocation. While the short-range echolocation calls allows the members of the SRE guild to obtain a better perception of the near surroundings and to better deal with background echoes, higher manoeuvrability helps them avoid collisions with obstacles in their flight path within vegetation. This finding is consistent with previous studies that reported guild-specific responses to vegetation structure (Jung et al. 2012) and confirmed that bats respond to habitat structure in functionally different ways.

Bat detection probability may be affected by vegetation density and call frequency because higher call frequencies travel shorter distances than lower ones due to greater atmospheric attenuation. This could have biased our interpretations of the relationship between bat activity and forest structural components. However, Yates and Muzika (2006) and Bender et al. (2015) showed that the probability of bat detection in forests was not related to vegetation density, although bat occupancy was. Moreover, Obrist et al. (2011) showed experimentally that foliage density only weakly (≈5%) attenuates calls at frequencies between 20-60 kHz, and the bat species we studied are not known to change call frequency substantially in relation to the habitat they preferably use. Of more concern is the likelihood that bats may reduce call intensity when flying in dense vegetation, making them less likely to be detected. Indeed, bats are likely to reduce call intensity in dense foliage to avoid acoustic masking by clutter echoes (Brinklov et al. 2010). Although we acknowledge that variation in habitat-dependent call intensity may bias our results to some extent, we are encouraged that the trends we document fit with expectations from flight morphology. For example species that use short-range

342 echolocation have wing shapes adapted for flying in cluttered situations and show higher levels of
343 activity in the forest interior, even though their call intensity may be lower there. Furthermore, any
344 decreases in bat detection probabilities caused by decreases in call intensity in dense vegetation may
345 be compensated by increased pulse repetition rates as bats may need more details of the acoustic
346 scene. Finally, it is also likely that the density of vegetation may affect the quality of the echolocation
347 calls recorded and thus their identification (O'Keefe et al. 2014), which might be more of an issue
348 when working at the species level. In our study, while bat identification was challenging (e.g.
349 similarity of calls between species, poor-quality calls) the clustering of species into guilds allowed us
350 to make a nearly complete use of our dataset: we were able to affiliate 99.6% of the bat sequences
351 recorded into guilds. Thus, we assume that the density of vegetation played only a small role in
352 affecting bat detectability relative to estimates of occupancy.
353
354 4.1.1. Bat activity in the forest interior
355 Our findings highlight an important variable, foliage height diversity (FHD), for SRE, MRE
356 and *P. pipistrellus* species. Since FHD represents the degree of scatter of vegetation heights along the
357 vertical forest profile, higher FHD values may negatively affect bat accessibility and manoeuvrability.
358 Thus, the negative correlations and relatively high effect sizes of FHD on the activity of MRE as well
359 as *P. pipistrellus* were expected. These findings corroborate several studies that show that, edge
360 specialist bat species avoid forests with highly scattered vertical vegetation profiles when foraging or
361 commuting (Adams et al. 2009; Brigham et al. 1997; Erickson and West 2003; Obrist et al. 2011).
362 Similarly, increased LAI, representing more closed forests, also affects activity of both these groups
363 negatively. However, while we hypothesized a positive relationship between FHD and activity for the
364 SRE guild (Norberg and Rayner 1987; Schnitzler and Kalko 2001), we found a negative relationship,
365 though with a relatively low effect size. This suggests that even bats with high flight manoeuvrability
366 concentrate their activity in vertically less complex forests. The most plausible reason for this finding
367 arises from the fact that all forests in the study area are managed according to principles of
368 sustainable, multi-purpose forestry (excluding plantations and monocultures) and thus, are strongly
369 limited in the gradient of observed FHD. Although we randomly selected the sampling sites, we

370 obtained a small gradient from moderate to high FHD values ranging from 0.84 to 1.28 (mean: 1.08;
371 SD: 0.10). Therefore bats with high manoeuvrability and short echolocation range belonging to the
372 SRE guild seem to show a preference for a scattered profile until a certain threshold, after which the
373 vegetation is too dense, restricting accessibility, manoeuvrability and, ultimately, their foraging
374 efficiency (Rainho et al. 2010; Schnitzler and Kalko 2001). There is now widespread support for this
375 hypothesis, regardless of the forest type investigated (Adams et al. 2009; Brigham et al. 1997; Müller
376 et al. 2013). FHD has originally been proposed to explain bird diversity and positive correlations are
377 usually found (Clawges et al. 2008; MacArthur and MacArthur 1961), implying that higher FHD
378 leads to greater niche diversity along the vertical gradient of the forest. Even though we are aware that
379 we used an adjusted version of the FHD concept and that we investigated bat activity and not bat
380 diversity, our results point out that the same forest structural attribute may have very different
381 ecological consequences for different taxa that utilise the same three-dimensional habitat space.
382 We further found canopy ruggedness to be important for the activity of bats from the MRE
383 guild, as well as for *P. pipistrellus*. As suggested in other studies (Jung et al. 2012; Kalcounis et al.
384 1999; Müller et al. 2013), bats may use the external canopy surface as a surrogate of edges when
385 commuting and foraging. Thus, for edge specialist bats such as *Pipistrellus* spp., higher heterogeneity
386 of the canopy surface provides greater benefits such as protection from predators, shelter from wind
387 (Verboom and Spoelstra 1999), and acoustic landmarks for commuting (Schaub and Schnitzler 2007).
388 Moreover, an increased canopy surface ruggedness may produce particular microclimatic conditions
389 favourable to a higher abundance of insects (Ulyshen 2011), thus indirectly affecting bat activity.
390 The height of the canopy had an effect on the activity of the LRE guild, as suggested by Dodd
391 et al. (2012) for lasiurine bats. However, given that *Eptesicus* spp., *Nyctalus* spp. and *Vespertilio*
392 *murinus*, which comprise the LRE guild, are known to forage or commute over the forests at high
393 altitudes or in open spaces (Vaughan et al. 1997), detectors placed in high canopies may be more
394 likely to record their echolocation calls (Müller et al. 2013), potentially introducing a recording bias.
395 Open space foragers are also more exposed to lower temperatures (e.g. dropping quicker during the
396 night in the open space than at edges or in the forest interior), which might explain their activity
397 showing stronger temperature dependence than e.g. the SRE-guild.

398 4.1.2. Bat activity in forest gaps

399 Vegetation height and canopy ruggedness were the main variables influencing LRE, MRE
400 and *P. pipistrellus* in gaps. Only the SRE guild was influenced by the ground vegetation cover,
401 probably reflecting the preferences of most *Myotis* species (except *Myotis myotis*; Arlettaz 1996;
402 Audet 1990) to forage above vegetated ground, e.g. when gleaning prey from leaves. As for the forest
403 interior, MRE and *P. pipistrellus* showed the same trend: in forest gaps these edge specialist bats
404 seem to prefer areas with higher vegetation heights. Given that we deliberately excluded heavily
405 overgrown gaps in our design to maximise detection of bats and to record high quality bat
406 echolocation calls for optimising bat acoustic identification (Obrist et al. 2004), the vegetation height
407 may be interpreted in terms of different early stages of forest regeneration. In a recent study, Müller et
408 al. (2012) demonstrated that the abundance of insect prey eaten by bats is vegetation-dependent, with
409 higher prey abundance in dense vegetation. This implies that gaps with rapid vegetation succession
410 may harbour more insects that thrive on the young plants or leaves, thus attracting more bats such as
411 LRE, MRE and *P. pipistrellus*, which forage in these open forest habitats. Higher insect abundance
412 may also result from favourable microclimatic conditions and heterogeneity of the vegetation
413 structure and composition, which provides a great diversity of microhabitats (Bouget and Duelli
414 2004). The ruggedness of the external vegetation surface is a good proxy for the heterogeneity of the
415 vegetation in the gaps and is likely associated with the availability and abundance of food.
416

417 **4.2. LiDAR provides unique habitat information**

418 Our results suggest that forest structure derived from LiDAR data provides ecological
419 information that is complementary if not superior to field vegetation survey data. Although
420 complementary effects of LiDAR-derived habitat variables in combination with field surveys are
421 documented for measuring forest bird habitats (Zellweger et al. 2014), the large difference in
422 ecological relevance we found explaining bat activity was surprising. A potential reason for this may
423 be related to how habitat is measured and how bats perceive and use forest habitats. Vegetation
424 surveys in the field normally involve visual inspection from an observer close to the ground. Thus,
425 several important aspects of the three-dimensional habitat space, such as upper canopy characteristics,

426 may remain concealed due to restricted visibility. LiDAR overcomes this restriction by measuring
427 forests from a "top-down" perspective, which in many cases is more similar to how bats perceive and
428 use forest habitats compared to the "bottom-up" view in field surveys. Thus, the high level of detail in
429 LiDAR data representing canopy characteristics provides novel opportunities to study species-habitat
430 relationships that were previously not readily available. Furthermore, LiDAR data gathered by the
431 same instrumentation and survey configuration will have less of an "observer bias" that is commonly
432 present in field data surveys where multiple people are involved. However, if LiDAR data were
433 acquired with different settings, the accuracy and precision of the derived variables need to be tested
434 and compared for the different settings.

435 Compared with datasets from either leaf-on or leaf-off LiDAR surveys, it appears that the
436 combined leaf-on and leaf-off dataset carried more ecologically relevant information about canopy
437 architecture and vertical forest structure for studying the activity of bats in mainly deciduous forests.
438 This was particularly apparent for canopy ruggedness and FHD, and their relatively large effects on
439 the activity of MRE and *P. pipistrellus*. Although canopy ruggedness frequently occurred in the top
440 models in the leaf-on model selection (Table S2), it was surprising that its effect was a lot stronger
441 when derived from combined leaf-on and leaf-off data. While such effects remain to be explored, they
442 are potentially influenced by the abundance of coniferous trees and the fact that leaf-off data may
443 contribute essential information about structural elements of the canopy other than foliage, such as
444 twigs or branches. FHD was best represented in the combined dataset as well, however, its effects on
445 bat activity were also evident when using the leaf-off data only. This suggests that leaf-off LiDAR
446 may be superior to leaf-on LiDAR in describing habitat attributes related to the vertical structure in
447 deciduous forests. As shown by Wasser et al. (2013), this is most likely related to the increased laser
448 pulse penetration through the canopy during leaf-off conditions, which enhances the detection of
449 subcanopy vegetation elements affecting the manoeuvrability of bats. As illustrated in Figure 2, the
450 increased canopy penetration during leaf-off conditions leads to an increased detection of vegetation
451 elements in the lowest forest strata, which includes tree regeneration and shrubs, both being essential
452 elements of vertical forest structure. The quality of LiDAR data for ecological applications in
453 temperate regions thus depends on the time of the year they were acquired. Although we show that

454 combined leaf-on and leaf-off data reveals the greatest potential for LiDAR applications in bat
455 ecology, our results support the recommendation that with limited budgets, acquiring leaf-off data is
456 preferable to leaf-on data.

5. CONCLUSIONS AND OUTLOOK

Bat activity is strongly influenced by forest vegetation structure and is also modulated by species-specific echolocation and flight characteristics. Although our correlative framework hampers conclusions about the effective drivers of the guild-specific activity patterns, our results support the assumption that factors related to canopy architecture and vertical forest structure have strong effects on bat habitat use. These effects can either be direct, e.g. via decreasing manoeuvrability in forest stands with highly scattered vegetation along the vertical profile, or indirect, e.g. via increased resource abundance and diversity in stands with a complex canopy architecture. LiDAR remote sensing provides information on forest structure that is difficult or impossible to collect in the field, especially across large areas. LiDAR thus substantially improves our abilities to reliably map the entire 3D habitat space in forests at a relevant grain size, to the benefit of future studies investigating the ecological relevance of canopy structure. Combined leaf-on and leaf-off data holds more ecologically relevant structural information than the two individual datasets, and leaf-off appears to be the preferable choice over leaf-on for limited budgets. With the recent development of new technologies and techniques such as miniature GPS devices and flight path tracking (Matsuo et al. 2014), extended use of LiDAR technology may push forward frontiers in the field of animal movement ecology, especially in structurally complex habitats such as forests.

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682

683 **TABLES**

684 **Table 1.** Variables describing the vegetation structure of the sites where we investigated bat activity in the forest interior (FI) and in forest gaps (gap).

Variable	Short description	Unit	Source	Plot type
Vegetation layers	Number of vegetation layers according to Keller (2011)	number	Field	FI
Snags	Number of standing dead trees with diameter at breast height > 25 cm	number	Field	FI and gap
Density of trees	Number of trees higher than 5 m per hectare	trees/ha	Field	FI
LAI	Leaf area index estimated from hemispherical photographs using Hemisfer 1.5 (Schleppi et al. 2007, Thimonier et al. 2010)	index	Field	FI
Understory vegetation clutter	Vegetation clutter measured with a profile board (Nudds 1977)	index	Field	FI
Shrub vegetation cover	Visual estimation of shrub vegetation cover, i.e. cover of shrubs and small trees between 1.3 and 5 m in height (Keller 2011)	%	Field	FI and gap
Ground vegetation cover	Visual estimation of ground vegetation below 1.3 m (Keller 2011)	%	Field	FI and gap
Mean vegetation height	Mean of vegetation point cloud	m	LiDAR	FI and gap
Maximum vegetation height	Maximum of vegetation point cloud	m	LiDAR	FI and gap
SD of vegetation height	Standard deviation of vegetation point cloud	m	LiDAR	FI and gap
Proportion of lower vegetation	The number of vegetation points between 1.3 m and 5 m divided by the total number of all vegetation points	%	LiDAR	FI and gap
Canopy cover	The number of vegetation heights above 20 m divided by the total number of all returns, including terrain points (Morsdorf et al. 2006)	%	LiDAR	FI
Mean canopy height	Mean of interpolated outer canopy surface with a pixel size of 0.5 m (see text for details)	m	LiDAR	FI
SD of canopy height	Standard deviation of interpolated outer canopy surface with a pixel size of 0.5 m (see text for details)	m	LiDAR	FI
Canopy ruggedness	Terrain ruggedness index (TRI, Wilson et al. 2007) applied on a 3x3 pixel window of the outer canopy surface with a pixel size of 0.5 m (see text for details)	index	LiDAR	FI and gap

FHD	Foliage height diversity adopted from MacArthur and MacArthur (1961) to measure the degree of scatter of vegetation elements along the vertical forest profile (cf. Clawges et al. 2008) (see text for details)	index	LiDAR	FI
Gap size	Area of gap	m^2	ArcGIS	gap
Edge structure	Visual classification of gap edge in either open or closed (Hamberg et al. 2009)	index	Field	gap

685

686 **Table 2.** Sum of guild- and species-specific bat activity (number of 5 min intervals with ≥1 bat
687 sequences) in 32 plots in the forest interior and in the forest gap, respectively. The two detectors in the
688 forest interior were located at both ground and canopy. SRE: short-range echolocators; MRE: mid-
689 range echolocators without *P. pipistrellus*; LRE: long-range echolocators.

Taxa	Forest interior (two detectors/site)	Forest gap (one detector/site)
SRE	**4,890**	**1,468**
Myotis bechsteinii	5	1
Myotis bechsteinii-brandtii	55	30
Myotis brandtii	59	31
Myotis brandtii-daubentonii	449	162
Myotis brandtii-mystacinus	220	93
Myotis daubentonii	507	156
Myotis daubentonii-emarginatus	63	19
Myotis daubentonii-mystacinus	452	118
Myotis emarginatus	293	43
Myotis emarginatus-brandtii	84	14
Myotis myotis	411	167
Myotis mystacinus	104	19
Myotis mystacinus-emarginatus	209	52
Myotis mystacinus-nattereri	45	11
Myotis nattereri	13	5
Myotis spp.	1,894	535
Plecotus spp.	27	12
MRE	**2,885**	**6,767**
Hypsugo savii	3	6
Pipistrellus kuhlii	408	616
Pipistrellus nathusii	890	3,254
Pipistrellus nathusii-kuhlii	312	670
Pipistrellus pipistrellus-nathusii	824	2,118
Pipistrellus pygmaeus	135	24
Pipistrellus pygmaeus-pipistrellus	312	72
Pipistrellus spp.	1	4
Pipistrellus-Hypsugo	0	3

LRE	**95**	**473**
Eptesicus spp.	45	183
Eptesicus-Nyctalus	8	41
Eptesicus-Vespertilio	0	7
Eptesicus-Vespertilio-Nyctalus	17	45
Nyctalus leisleri-Vespertilio murinus	0	1
Nyctalus spp.	25	177
Nyctalus-Vespertilio	0	15
Vespertilio murinus	0	4

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692 **Table 3.** Variables and their relative importance (effect size) represented by the Estimate from GLMMs relating standardized variables of forest vegetation
693 structure to the activity of different bat guilds and *P. pipistrellus* in the forest interior and the forest gaps. SRE: short-range echolocators; MRE: mid-range
694 echolocators without *P. pipistrellus*; LRE: long-range echolocators. The results are reported for each of the dataset containing variables recorded in the field
695 and the respective LiDAR variables (leaf-on, leaf-off and combined).
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Model	Variable	Leaf-on				Leaf-off				Combined leaf-on leaf-off			
Forest interior		**Estimate**	**SE**	***t***	***P***	**Estimate**	**SE**	***t***	***P***	**Estimate**	**SE**	***t***	***P***
SRE[a]	FHD	-0.18	0.08	-2.36	*	-0.22	0.07	-3.01	**	-0.20	0.07	-2.66	**
	Density of trees	-0.18	0.08	-2.30	*	-0.20	0.08	-2.70	**	-0.19	0.08	-2.47	*
	Temperature	0.02	0.01	1.70	.	0.02	0.01	1.78	.	-	-	-	-
MRE[a]	FHD	-	-	-	-	-0.30	0.14	-2.18	*	-0.42	0.14	-2.94	**
	Canopy ruggedness	-	-	-	-	0.28	0.13	2.13	*	0.48	0.15	3.22	**
	Mean canopy height	0.30	0.15	2.03	*	-	-	-	-	-	-	-	-
	LAI	-0.33	0.15	-2.24	*	-	-	-	-	-	-	-	-
LRE[b]	Mean canopy height	0.72	0.23	3.12	**	0.71	0.24	2.99	**	0.72	0.23	3.11	**
	Temperature	0.11	0.04	2.68	**	0.11	0.04	2.67	**	0.11	0.04	2.68	**
P. pipistrellus[a]	FHD	-	-	-	-	-0.28	0.14	-2.02	*	-0.44	0.14	-3.21	**
	Canopy ruggedness	-	-	-	-	-	-	-	-	0.56	0.14	3.94	***
	LAI	-0.40	0.14	-2.83	**	-0.40	0.14	-3.00	**	-0.37	0.12	-3.02	**
	Temperature	0.05	0.03	1.70	.	0.05	0.03	1.68	.	-	-	-	-
Forest gap													
SRE[a]	Ground vegetation cover	0.19	0.07	2.54	*	0.19	0.07	2.54	*	0.19	0.07	2.54	*

MRE[a]	Mean vegetation height	0.22	0.12	1.88	.	0.29	0.12	2.46	*	0.27	0.12	2.26	*
LRE[b]	Canopy ruggedness	-	-	-	-	-	-	-	-	0.32	0.13	2.37	*
P. pipistrellus[a]	Mean vegetation height	0.31	0.11	2.91	**	0.34	0.10	3.27	**	0.33	0.10	3.21	**

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699 SE: standard error.

700 [a]GLMMs with a negative binomial distribution.

701 [b]GLMMs with a Poisson distribution.

702 . $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

703 FHD: foliage height diversity; LAI: leaf area index

FIGURES

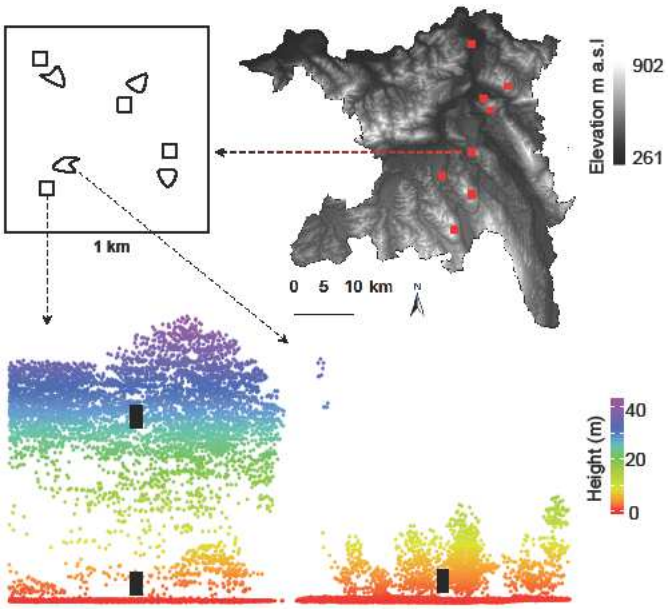

Fig 1. Sampling design showing the eight 1-km^2-sampling squares (red squares) in the elevation model of the study area (top right). The nested plot design within each km^2 (top left) includes four plots in the forest interior (small black squares) and the four corresponding gaps (small black polygons). The bottom figures show normalized LiDAR point clouds representing the forest floor and the 3D distribution of vegetation elements, as well as the location of the bat loggers (black boxes) in each plot. We placed two loggers in the forest interior (bottom left) and one in the forest gap (bottom right).

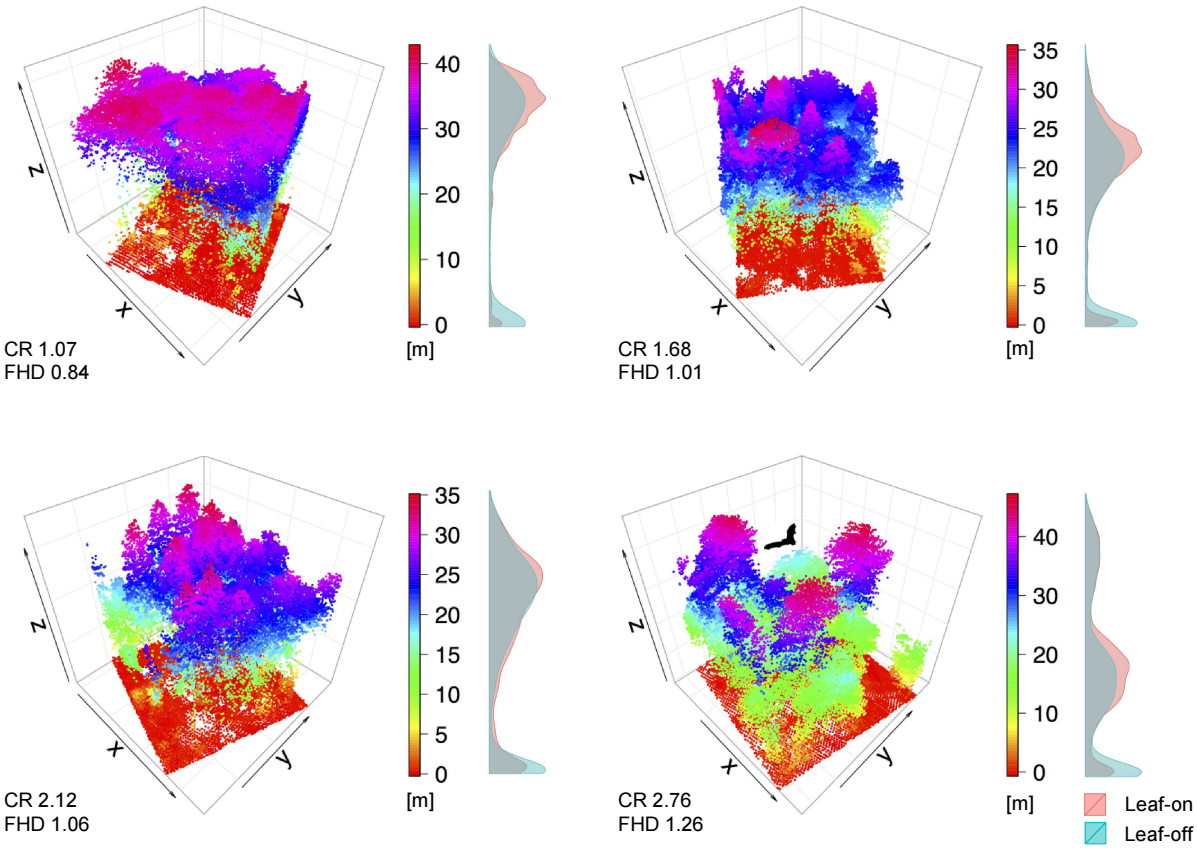

Fig 2. Normalized LiDAR point clouds from the combined leaf-on and leaf-off dataset for four plots along a gradient of canopy ruggedness (CR) and foliage height diversity (FHD). The distribution of return heights (in meters) along the vertical profile is shown by vertical density plots for the leaf-on and leaf-off datasets separately, using the same scale as for the coloured scale bars.